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A simulation approach to studying the relationship between landscape features and social system on the genetic structure of a tamarin primate population

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A simulation approach to studying the relationship between landscape features and social system on the genetic structure of a tamarin primate population

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Abstract

The interplay of landscape features and social system on the genetic structure of a primate population: A simulation study using tamarin monkeys

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Landscape genetics is an emerging field that seeks to understand how specific landscape features and microevolutionary processes such as gene flow, genetic drift, and selection interact to shape the amount and spatial distribution of genetic variation. This study explores, through agent based simulations, how the specific mating and social system of tamarin primates (genus *Saguinus*) influences population genetic structure and patterns of relatedness within and among groups of this primate species, which might affect the ability of landscape genetic studies to detect the effects of fragmentation on gene flow. I use a spatially-explicit agent-based population genetics simulation model (GENESYS) configured to reflect the particular social system of tamarin monkeys (i.e. small group size, limited numbers of breeders per group, frequent twin births, and short dispersal distances) to assess whether the isolation by distance model of genetic differentiation expected in an unfragmented landscape can be distinguished from the isolation by barrier model expected in a fragmented landscape. GENESYS allows a user

to explore the effects of social structure and landscape features on the population genetic structure of social animals, such as primates. I simulated two different landscapes containing an otherwise equivalent population of tamarins. In the first setup I simulated a homogeneous landscape unconstrained by any barriers to gene flow, while for the second setup, a barrier to gene flow restricted dispersal from one half of the landscape to the other. I found that the particular mating system of tamarin results in the rapid genetic differentiation of its social groups and consequently its populations. Social groups in the continuous landscape indeed revealed an isolation by distance pattern, while social groups on the fragmented landscape yielded instead an isolation by barrier model, where the barrier rather than geographic distance per se influenced the spatial genetic structure of the population. The results from this study suggest that features of the tamarin social system influence population genetic structure, which could affect the ability of landscape genetic studies to detect the effects of fragmentation on gene flow. To more fully address that issue, future studies should focus on a range of different primate social systems.

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INTRODUCTION

Habitat fragmentation is one of the major causes of biodiversity loss and species extinction. It is a process in which a continuous habitat of a particular type (e.g., forest) is modified into smaller and partially or completely isolated patches of that habitat type that are separated from one another by a matrix of one or more different habitat types, resulting in a heterogeneous landscape (Noss et al., 2006). The resulting decrease in area of the original habitat type, and the increase in distance between patches, reduce the functional connectivity between patches and can restrict individual dispersal or gene flow among patches. With restricted gene flow, habitat fragmentation can lead to changes in microevolutionary processes that include greater levels of inbreeding, loss of genetic diversity within fragments and an increase of the genetic differentiation among fragments (Frankham et al., 2002). These processes can ultimately cause the erosion of a species' evolutionary potential and increase the probability of extinction in the long term (Frankham, 2005). Consequently, species persistence is determined by the ability of members of that species to disperse across a heterogeneous landscape and, in turn, by their ability to maintain connectivity (i.e. the degree to which the landscape impedes or facilitates movement among resource patches) (Taylor and Fahrig, 2006). Therefore, understanding how landscape features influence population structure and genetic diversity for organisms distributed across a fragmented landscape is of major importance to determine conservation units and design and implement new areas of conservation (Lindenmayer et al., 2008).

Nonetheless, investigating the influence of the landscape on individual dispersal by traditional approaches, such as mark-recapture or radio tracking methods, is difficult. These methods require the sampling of large number of individuals, can be time

consuming, and are not easily applicable to endangered species (Cushman, 2006). Genetic data, on the other hand, offer a non-invasive alternative strategy to infer patterns of dispersal. Landscape genetics is an emerging field that combines population genetics, landscape ecology, and spatial analysis (Manel et al., 2003). It seeks to understand how specific landscape features and microevolutionary processes such as gene flow, genetic drift, and selection together interact to shape the amount and spatial distribution of genetic variation (Sork et al., 2010; Sork and Waits, 2010). The key distinction between landscape genetics and other kinds of population genetic studies is that the former includes spatially explicit research that quantifies the effects of landscape composition, configuration, and matrix quality on gene flow and spatial genetic variation (Storfer et al., 2007). In comparison to traditional population genetics studies, when taking a landscape genetics approach, the land between patches is not considered as just a geographic distance but rather is recognized as a major determinant of biological and ecological processes. Therefore, landscape genetics studies take into account the relative influence of landscape characteristics – fundamentally its heterogeneity – in considering connectivity and genetic variation within and among populations (Balkenhol et al., 2009; Holderegger and Wagner, 2006, 2008b).

In a landscape genetics approach, the genetic characteristics of many individuals sampled across large areas can be directly associated with a hypothesis of connectivity. Thus, a primary goal of this type of analysis is to infer the causal relationship between the process of gene flow occurring over a landscape and the subsequent patterns of genetic variation that arises (Holderegger and Wagner, 2008a). However, inferring causation from observing a correlation between a landscape feature and a genetic pattern can be dangerous due to the potential for spurious correlations to exist between the model under evaluation and untested alternatives (Shirk et al., 2012). Correlation alone does not imply

causation (Hilborn and Stearns, 1982), and the proposed landscape variable explaining the spatial genetic structure of a population may be unrelated to the true driver of genetic differentiation (Shirk et al., 2012). Consequently, if the causal mechanism is not evaluated as a model variable, and instead attention is focused on this correlated variable, researchers are at risk of making incorrect inferences about the pattern-process relationship. If this is case, then the true driver of some observed landscape genetic pattern might be misidentified or obscured, and conservation efforts in the case of endangered species can be misinformed (Segelbacher et al., 2010).

One step towards minimizing the risk of making incorrect conclusions in landscape genetics studies is by using population genetic simulations. Simulation-based approaches are simplified representations of a reality that serve to express as clearly as possible how one believes that reality works. They provide flexibility and generality, allowing a researcher to specify how landscape and demographic factors are expected to govern gene flow and then evaluate if empirical patterns of isolation match those generated under simulation (Epperson et al., 2010). In other words, evaluate whether there is a good match between the pattern-process relationship observed with the hypothetical explanatory variable and the relationship observed with the true one. By explicitly controlling pattern-process relationships, simulations enable a rigorous assessment of the different possible causes that determine population genetic structure, which is not possible in empirical studies (Epperson et al., 2010; Shirk et al., 2012).

Individual- or agent-based simulation modeling is an approach that begins at the individual level and is based on a set of rules that determine the outcome of the interactions between an individual agent and its environment or among agents, based on specified behavior rules (Gilbert, 2008). Thus, it is a spatially explicit approach that provides a framework that allows researchers to generate an expectation of population

structure based on these behavioral rules and in the context of the specific landscape in which a set of individuals are found. Consequently, it allows the comparison and evaluation of multiple landscape scenarios, enabling linkage between empirical analysis and simulation modeling.

Simulations, therefore are a powerful tool to reduce the potential of false inferences. However, only until recently simulations have begun to be used in landscape genetics. Most simulation studies have focused on evaluating the effect of landscape complexity on genetic differentiation. For example, Bruggeman et al. (2010) used simulation models to evaluate the influence of patch size and patch isolation on the abundance, effective Ne, and Fst of woodpeckers. Cushman et al. (2012) investigated the relative influence of habitat area and fragmentation on genetic differentiation, and Oyler-McCane et al. (2012) assessed the effect of study design and sampling scheme on landscape genetic inferences. However, no simulation study thus far has explored the effect of life history characteristics or mating system on landscape genetic patterns.

The emergence and maintenance of spatial genetic patterns are influenced by many highly dynamic factors, making the analysis of landscape genetic relationships very complex. Demographic dynamics, spatial ecology, and social behavior and their interaction with environmental heterogeneity are coupled with sources of genetic variation that are more commonly considered in population genetic studies (e.g., gene flow, drift, mutation and selection), to produce the true landscape-genetic relationships (Balkenhol and Landguth, 2011). Specifically, the ecology and behavior of an organism, as well as the habitat where it lives and its associated spatial complexity, all can influence how genetic diversity is spatially structured among populations. Features of social systems such as sex-biased dispersal, dominance hierarchies, strong reproductive skew and patterns of new group formation all influence how individuals within groups and

within populations are related to one another and, in turn, likewise influence the population genetic structure (Chepko-Sade and Halpin, 1989; Chesser, 1991; Di Fiore, 2012a; Melnick, 1987; Storz, 1999; Sugg et al., 1996). These aspects of the social system, which are products of the differences in behavior among individuals and between sexes, subsequently have profound consequences for the genetic structure of populations (Di Fiore, 2012a; Melnick, 1987).

Among primates for example, dispersal is one of the principal factors that influence how a taxon's genetic variation is distributed across space and among social groups. If, for example, two groups of individuals interchange dispersing individuals more often with one another than with other adjacent groups then the resulting genetic structure of the population can be very different than if individuals are transferring among all the groups at random. In other words, if dispersal abilities and distance are relatively low and short, over time those groups that are geographically close and exchange individuals frequently should come to be similar to one another genetically and show relative high mean between group relatedness while becoming differentiated from other groups (Wright, 1943; Di Fiore, 2012a). Additionally, if there is strong reproductive skew and a single male or female are responsible for parentage of most of the offspring born in a social group over some period of time, then individuals belonging to similar age-cohorts born during that individual's tenure should be more closely related to one another, on average, than they are to individuals in the group that are less similar in age (Di Fiore, 2012a). Consequently, strong reproductive skew and short dispersal distances should lead to high genetic differentiation among social groups in a local population.

So far, simulation models have incorporated simplifying assumptions about mating system and subtler aspects of life history (Epperson et al., 2010), even though there is ample empirical evidence that they can alter spatial genetic structure (Ross, 2001;

Storz, 1999). Landscape genetic models have added the effects of landscape features on biological processes such as dispersal and mating systems, however they lack the integration of these processes with the biological realism of individual behavior and population dynamics (Epperson et al., 2010). Consequently, it is essential to integrate information regarding behavioral ecology with other aspects of the mating system and social structure that will influence gene transmission. The goal of this study is to evaluate how individual spatially explicit space use behavior impacts gene flow and resulting genetic patterns. More specifically, this study uses an agent-based model to explore how the specific mating and social system of tamarin primates (*Saguinus* sp.) influences population genetic structure and patterns of relatedness within and among groups of this primate species and, in turn, affects the ability of landscape genetic studies to detect the effects of fragmentation on gene flow.

Tamarin monkeys' specific social structure has normally been described as an extended family with strongly skewed reproduction among both females and males due to monopolization of breeding by a single male and female within each social group (Goldizen, 1988; Goldizen, 1990; Goldizen and Terborgh, 1989; Huck et al., 2004a; Tardif et al., 2008; Tardif et al., 1990; Terborgh and Goldizen, 1985). Tamarin social groups are typically composed of a breeding couple plus mature offspring or siblings of the breeding pair that remain in the group and may assist the rearing of the young. As a result, it is expected to observe higher overall genetic relatedness within groups than between groups. Accordingly, it could be predicted that the polyandrous communal breeding system strongly skewed towards a single male and the high within group relatedness seen in tamarins will lead to fine scale population structure (Huck et al., 2007). Consequently, it could also be expected to observe a relative influence of social system on the effect of habitat fragmentation on gene flow.

This study evaluates how social organization exerts an influence on the apportionment of the genetic variation in a population and can potentially obscure landscape influences on the spatial patterning of that variation using as a model the social system of tamarin primates. The objective of this study therefore, is to evaluate whether tamarins' social system affects the capacity to correctly identify the generating landscape process. To evaluate this, I explored the effect of a continuous versus a fragmented landscape on the genetic population structure of tamarin social groups modeled under the parameters of their specific social and mating system. In the continuous landscape, it is expected that genetic isolation accrues as a function of distance (isolation by distance or IBD), particularly in landscapes where migration rates are relatively unaffected by landscape heterogeneity (Wright, 1943). On the contrary, in a fragmented or discontinuous landscape, where dispersal is affected by landscape heterogeneity, populations may exhibit substructure that arises either by strong migration barriers that sharply reduce gene flow (isolation by barrier or IBB) (Ricketts, 2001) or by the intrinsic heterogeneity of the landscape that causes isolation by resistance (IBR) (McRae, 2007). Here, I assessed whether the isolation by distance model expected in an unfragmented landscape can be differentiated from the isolation by barrier model expected in a fragmented landscape divided by a barrier, for a species with a tamarin-like mating system.

METHODS

To evaluate the sensitivity of landscape genetic inference to tamarin's social system, I simulated the effect of their particular mating system on population structure using an agent-based model called GENESYS. GENESYS (Di Fiore, 2010, 2012b) is an agent-based population genetics simulation toolkit that allows a user to explore the effects of social structure and landscape features on the population genetic structure of social animals, such as primates. Agent-based simulation is a bottom-up approach that explicitly considers the components of a system and attempts to understand how the system's properties emerge from the interaction of these components (world, model and agent) (Grimm et al., 2006; McLane et al., 2011). Agents are goal driven and can respond to changes in the environment, adapting their state and behavior in response to other agents and the environment itself and by explicitly executing decision-making heuristics, which are a set of rules that can be predefined or learned through experience or feedback with other agents and the environment (Semeniuk et al., 2011). GENESYS therefore allows the examination of how system level properties (population genetic structure and dispersal patterns) emerge from the behavior of its agents (as determined jointly by the landscape and features of the social and mating system).

Tamarins

Tamarins, along with marmosets, belong to the neotropical primate Family Callithrichidae and are unusual among primates because of their unique social characteristics (French, 1997). They live in small, multimale-multifemale groups with a functionally polyandrous breeding system in which only one female gives birth within the group, although she may copulate with more than one male (Ferrari and Lopez Ferrari,

1989; French et al., 1989; Garber et al., 1993; Goldizen, 1987; Goldizen, 1988; Goldizen, 1990; Huck et al., 2004a; Sussman and Garber, 1987). Twinning is common among these species, and there is communal care of the young provided principally by adult males, but other group members can also provide care (Tardif et al., 1993). This "communal breeding system" is characterized by extra individuals or helpers that participate in the carrying and feeding of young. Helpers are often reproductively mature individuals that do not breed but who nonetheless provide help by carrying and providing food to infants (generally their younger siblings) (Brown, 1978; Emlen, 1991; Skutch, 1935). Faaborg and Patterson (1981) coined the term "cooperative polyandry" to describe this type of group where two or more males copulate with a single female during a single breeding season and then cooperate to raise the female's subsequent offspring (Goldizen, 1988). In tamarins, various examples of this cooperative breeding come from studies of *S. fuscicollis* (Goldizen and Terborgh, 1989), *S. myxtax* (Garber et al., 1993), *S. imperator* (Baker and Woods, 1992) and *L. rosalia* (Bales et al., 2001), where groups were composed of adults of both sexes characterized by a single female having a single set of offspring at a time, which are then cared for by all of the adults. Nonetheless, within the family there is an unusual flexibility in their mating systems, with polygyny and monogamy occurring in addition to polyandry (Ferrari and Lopez Ferrari, 1989; Goldizen and Terborgh, 1989; Hilborn and Stearns, 1982; Sussman and Garber, 1987).

Studies of mustached tamarins (*S. myxtax*) have given further evidence of a polyandrous mating system. Despite having evidence of the breeder female mating with multiple males, in the groups studied the same male sired 92.9% of the infants in the group (Huck et al., 2004a; Huck et al., 2004b; Huck et al., 2007). Additionally, mean relatedness of females and males in this study was significantly higher within than between groups (mean $R = 0.31$).

The model

GENESYS simulates population dynamics and the spatial apportionment of genetic variation within and between social groups of primate species in a heterogeneous landscape by tracking individuals through time. The model allows overlapping generations, sex-biased dispersal patterns, reproduction largely within defined social groups, different mating systems, and variable levels of reproductive skew among males of nonhuman primates. Additionally, it allows different levels of habitat permeability and predation risk on animal movement and mortality as well as different dispersal models. Moreover, GENESYS allows several levels of social structure to be specificied; the world can contain multiple "populations", each of which can contain one or more social groups.

Mating and reproductive system

GENESYS allows the user to choose between three different mating systems depending on the number of males that can be specified as the sire. In the 'unimale' system, the model only assigns the most dominant male in a social group as the sire. On the contrary, the 'mm-dom-based' and the 'mm-based' systems allow the assignment of paternity to more than one male. However, the 'mm-dom-based model' takes into account the proportion of males mating as well as a measure of reproductive skew, parameters that the user is able to modify as well. A male skew value of 0, assigns an equal opportunity of reproducing to every male in a social group, while a value of 1 assigns all paternity to the most dominant male of a social group. In all the mating models, only those males who are not dispersing can reproduce. Nonetheless, the user can specify whether the possible sires are from the same social group as the female breeder or come from outside of the group. In the latter case, under each mating system, GENESYS

will choose the possible sire from the total population rather than from the same social group as the breeder.

In the case of females, GENESYS simulates breeding only by non-juvenile females who do not have an offspring and are not dispersing; these females reproduce based on rate given by their age-specific fertility. Every time a female reproduces, GENESYS creates a link connecting that female with her infant. However once that infant ages to beyond the juvenile stage (defined as ¼ of the maximum lifespan), this link is broken and the breeder female is allowed to reproduce.

Dispersal behavior

GENESYS allows the simulation of several different dispersal models, characterized by a different set of rules. In the 'stepping stone' dispersal model, for example, dispersers move to the closest social group that is either in their own population (if there is only one population) or in the closest population to their own. In the 'island' dispersal model, agents will disperse to any other social group in world. In the 'social dispersal' model, agents choose as their dispersal target the group with the greatest number of excess members of the opposite sex of reproductive age. Finally, in the 'random walk' model, disperses choose a random direction and disperse in that direction.

Genotype assignment

GENESYS randomly assigns genotypes to all individuals in the population. The user can simulate up to 99 loci and 99 alleles and can specify the allelic frequencies in the initial gene pool. Genotypes for immigrants (see below) are chosen at random based on current allele frequencies in the population into which an immigrant was moving.

Tamarin model parameters

Since this study uses as a model a tamarin species mating and social system, parameters were chosen for GENESYS simulations based on wild and captive studies of tamarin and marmoset species, to emulate their specific life history characteristics and breeding and mating system. Tamarins' lifespan, in general, averages 9 years (Tardif et al., 2008) and individuals from *S. oedipus* typically reach sexual maturity when they are 1.5 years (Ginther et al., 2002) with an average age of reproduction in golden lion tamarins (*L. rosalia)* that ranges from 2 to 6 years (Bales et al., 2001) and in saddle back tamarins (*S. fuscicollis*) from 2 to 4.5 years (Goldizen and Terborgh, 1989). Moreover, in *S. fuscicollis,* for example, infants stop weaning around 6 months of age, after which they become juveniles. Once they have reached one year of age they become subadults, and subadulthood lasts roughly one year (Goldizen, 1987). As a consequence, in the model each individual was given a maximum lifespan of 10 years and eight different age categories were specified (Table 1). Additionally, individuals reproduced only after transitioning to being "non-juveniles" (i.e., subadults or adults), or in other words, only those individuals that reached a quarter of their lifespan (2.5 years), were considered sexually active.

Mating and reproductive system

To simulate the tamarins' mating system, the breeding male and female of each social group, were specified as the single most dominant individual of each sex, where dominance was defined as a function solely of age. Although not many studies have been conducted on male tamarins, and not much is known about their reproductive patterns, the male mating system was modeled in GENESYS as 'mm-dom-based'. Dominance was modeled using a triangular function, where peak dominance is reached around 3/4 of the

lifespan, i.e., at roughly age 7.5 years. The proportion of males mating was 1, and to avoid having more than one male breeder per sex in each social group a male reproductive skew of 1 was assigned. Only those males who were not dispersing and were from the same social group as the female breeder were able to sire. Breeder females on the other hand, were not defined based on a reproductive skew value, but based on their age and age of their female groupmates.

Captive studies in marmosets have shown that age-specific fertility displays an inverted U-shaped form with a distinctive decline in the number of females producing offspring in the later half of life. However of those females that reproduce, there is no significant relation of age to interbirth interval (Caro et al, 1998). In contrast, Bales et al. (2001) reported no evidence for age related decline in fertility in wild *L. rosalia*, as assessed by the number of offspring born and reared per year. Studies on wild *S. myxtax* and *S. fuscicollis* indicated that 80% of groups containing more than one adult female only the oldest females was reproductively active (lactating and or pregnant) (Garber and Teaford, 1986). Additionally, tenure for common marmoset (*C. jacchus*) female breeders varies from 18 to 69 months, averaging 42 months, starting when females are around 4.5 to 5 years of age and ending when females are approaching 8 to 9 years (Tardif et al., 2008). So, although tenure of breeding females is highly variable in tamarins, (i.e. in *S. fuscicollis* it ranges from 3 weeks to 66 months (Goldizen and Terborgh, 1989; Terborgh and Goldizen, 1985), to simplify the model, it was assumed that tenure lasted until death. Consequently, in GENESYS from the moment a female reached half of her lifespan, her dominance was assigned to its highest value, and that level of dominance was maintained until she died. Nonetheless, only those females who had no offspring, were not dispersing, were not only the most dominant but also the oldest one in each social group were allowed to breed. So, even though at any given point of time there could be more

than one female older than 5 years of age in a group (and that, in turn, could have equally high dominance), there was only a single breeder female, the oldest of the residents. Once this female breeder died, a new dominant female, who was often the daughter of the previous one, was defined as the new breeder as a function of age. In wild populations, the death of the breeding female is typically followed by the immediate return from another group of a previously subordinate female, and in *S. oedipus* studies in captivity it has been seen that the onset of the normal ovarian function in the older daughter in a family group follows the death or removal of the breeding adult female (French, 1997; French et al., 1984; Heistermann et al., 1989).

In the model, females reproduced according to their age-specific fertilities that reflect the social system of tamarins (Table 1). Based on limited field data, it has been observed that female callitrichines begin reproducing well after they are presumably sexually mature (Goldizen and Terborgh, 1989) . Similarly, Bales et al. (2001) report an age of first reproduction in golden lion tamarins (*Leontopithecus rosalia)* of 3.6 years. Captive studies on marmoset colonies have suggested a mean age of first birth of 2.91 years as well as an average of 3.66 infants produced by a female per year of their reproductive lifespan and 1.28 weaned infants per year (Smucny et al., 2004). Additionally, the total number of infants produced by a breeder female in these colonies ranged from 1 to 60 infants, with a mean of ~8.0 (Smucny et al., 2004). Consequently, GENESYS was set so that females potentially start to reproduce at age 2.5, show peak fertility at age 5.0, and show a gradual decline in fertility between that age and the maximum lifespan. Interbirth intervals in tamarins are on average less than a year, 8-13 months in *Saguinus* sp (Dunbar, 1995) and 5.7 months in *C. jacchus* (Tardif et al., 2008), and females have on average 2 litters per year (Tardif et al., 2008). Therefore, in

GENESYS, females were set to twin every time they reproduced, with interbirth intervals of one year; one of the twin offspring was arbitrarily chosen as firstborn.

Dispersal behavior

Saguinus fusicollis males and females in Manu National Park dispersed equally and 44% of the emigration events occurred to adjacent groups (Goldizen and Terborgh, 1989). As a result, in GENESYS, I modeled dispersal by both sexes following a stepping stone model. The probability of dispersal assigned for both sexes was 0.5 as wild *S. fuscicollis* have been reported to have a 1:1 sex ratio of dispersers, with no sex difference in migration distance. As a simplification, the dispersal probability per every model tick (equivalent to one month) was assigned by dividing the overall dispersal probability by the number of "post-juvenile" ticks for a maximally aged individual. For both sexes, only non-juvenile individuals that were not the oldest or most dominant ones were allowed to disperse, as wild studies suggest that breeders seldom leave the group. In the case of females, only those without dependents were included in the pool of possible dispersers. Finally, although among tamarins some animals are known to disperse more than once (Goldizen et al., 1996), most disperse only one time, and thus for simplicity in the model animals were constrained to a maximum of one dispersal event during their lifespan.

Immigration

Because in wild populations, new immigrant individuals sometimes join a population from outside of a study area, I set up GENESYS to allow immigration of individuals of both sexes. Immigrants were modeled to appear at random position on the periphery of the world and moved into the world following a different dispersal model from the animals already present. In this case, immigrants chose as a target social group,

a group within the population into which they were moving that contained the fewest number of non- juvenile individuals of their same sex present, i.e., where they would face the fewest same-sex competitors for a breeding position. In this case, immigrants first identified those social groups that had the fewest number of adults and subadults of their own sex, and from those social groups chose the closest one. By allowing this type of dispersal, the model assured the recolonization of social groups and prevented the extinction of the whole population, while at the same time assuming that immigrants, like residents, preferentially move to a closer group when such an option is available.

Immigrants' sex was set by the relative dispersal rates of males and females. In this case, the sex ratio of immigrants was set at 1:1. Immigrant genotypes were chosen at random based on the population allelic frequencies. GENESYS was programmed to frequently update population allele frequencies (every 24 time steps, equivalent to every 2 years), and immigrant genotypes were drawn from these updated frequencies. Thus, immigration per se is not expected to be a significant force influencing population genetic structure.

Landscape Features

GENESYS allows a user to provide a spatially explicit landscape for the world in which the simulation takes place. The world is composed of 501 by 501 pixels, with each pixel corresponding approximately to 8m x 8m. Different pixels in this world can be assigned characteristics that influence the probability of dispersal through or across them. To simulate the effect of landscape quality on dispersal decisions, the landscape pattern was represented as a resistance surface with grid cell values representing costs of movement through the landscape. Each pixel in the landscape was thus assigned a "permeability" value (0 – 1), assigned to reflect its suitability and habitat quality. Before

each time step during dispersal, each dispersing individual assessed the average permeability of the patches from 0 to 10 pixels ahead that are between its current location and that of the group to which it is dispersing. If the average permeability of those 10 pixels evaluated was less than 0.5 (an arbitrary cutoff value used in this study), the individual turned one degree at a time, up to 180 degrees, and reassessed the permeability of pixels on the path ahead. If after turning 180 degrees an individual did not find a way forward with sufficiently high permeability (greater than 0.5), it died. Once an individual reached the border of the 'world', it followed a reflecting behavior, where individuals redirected their movement back into the world and moved 10 pixels in that direction.

Mortality and Population Regulation

Mortality was modeled stochastically in GENESYS and was based on age and sex specific probabilities, and, like female fertility, is incorporated into the simulation from a user-specified table of vital rates (Table 1). I based the mortality rates used in the simulations loosely on information available for wild groups of *Saguinus fuscicollis* in Manu National Park (Goldizen and Terborgh, 1989). However, mortality risk was also habitat dependent, and each patch in the landscape had a mortality risk assigned to it based on habitat type. For simplicity, mortality risk was modeled as inversely proportional to permeability: the more permeable the landscape, the lower the mortality risk. Moreover, if the infant of the breeding females died, they were automatically assigned as dependant free so that they could reproduce again. Additionally, if a breeder female with an infant died while in a social group, their offspring stayed alive. Finally, the maximum number of individuals present in the population at the end of every model year (12 time steps) was regulated. If the population size at that point in time exceeded the initial starting population size, excess individuals were killed off at random

Modeling scenarios

Two different scenarios were simulated, an unfragmented ("null" scenario) (Figure 1) and a "fragmented" landscape characterized by having an insurmountable barrier ("alternative" scenario) (Figure 2). To do this, I established a simulated world of ~1600 hectares in area (or ~4000m x ~4000m) containing the home ranges (~27 ha) of 36 social groups of 'tamarins' spread out on a hexagonal grid such that each social group was surrounded by up to six equidistant groups of neighbors (Figure 1). In the null scenario, 1 population, with 36 social groups was modeled in a continuous landscape with no fragmentation. In the null scenario, every pixel cell in the simulated landscape had the same permeability and mortality value assigned to it, and consequently individuals could move freely through the environment (Figure 1). This provided the baseline prediction of the expected population differentiation in the absence of any differential resistance in the landscape, or an "isolation by distance" model. In the alternative scenario, an unpassable barrier divided the initial population of the null scenario into two separate populations each one containing 18 social groups, respectively. In this scenario, the barrier inhibited the dispersal of individuals between populations and the landscape was coded as a binary grid cell (1 forest, 0 matrix). This scenario represented the expected "isolation by barrier" model.

Simulation and model output

The simulation model was run 100 times for 200 years (2400 time steps) for both the "null" and "alternative" conditions. Although group composition and sex ratio varies substantially among tamarin species, for this model the simulation started with social groups composed of 8 unrelated founders with a 1:1 sex ratio. For example, *S. fuscicollis*

social groups in Manu National Park have ranged from 2 to nine individuals, with a mean of five (Goldizen and Terborgh, 1989), while *S. oedipus* groups normally range from 1 to 19 individuals with a mean of approximately 6 individuals (Dawson, 1977; Neyman, 1977) and *S. myxtax* groups from 1 to 16, with an average group composition of 5 to 6 individuals (Garber et al., 1993; Ramirez, 1984). Regarding sex ratio, most tamarin species are characterized by having slightly male biased sex ratios, however the percentage of males is not very different than that in females. For example, the percentage of males in *S.myxtax* social groups ranges from 42.9% to 56.2% (Garber et al., 1984; Goldizen and Terborgh, 1989; Ramirez, 1984), while in *S. oedipus* is around 54% (Neyman, 1977). However, among adults in *S. fuscicollis*, specifically, groups tend to have 2 adult males and 2 adult females (Dawson, 1977).

Genotypes of each individual at the start of the simulation were assigned randomly using 20 loci with 20 alleles per locus. Every allele in each locus used to simulate each individual's genotype had an initial frequency of 0.05. In total 288 individuals were simulated and the demographic structure was composed of 4 age-classes based on *S. fuscicolli*s studies (Goldizen, 1987; Goldizen and Terborgh, 1989): adults (51% if the population), subadults (14%), juveniles (15%) and infants (19%). Each of the 8 age categories simulated had a specific probability of fertility and mortality (Table 1). These probabilities were determined based on captive and wild studies of tamarin and marmoset populations (Tardif et al., 2008). For example, female and male adults' as well as juvenile's probability of mortality was assigned based on *S. fuscicollis* studies in Manu National Park, where survival patterns were measured based on number of disappeared individuals that were assumed to be dead (Goldizen and Terborgh, 1989). As noted above, interbirth intervals were assumed to be one year, and each breeder female produced on average one pair of twins every year, based on the probability of fertility

assigned to the category it corresponded to (Table 1). Offspring's sex was randomly assigned following a 1:1 sex ratio. For each landscape scenario, 100 replicate simulations were conducted and the demography of each social group and population as well as each individual's genotype were updated every model year. Each simulation was run using the same initial parameters (Table 2).

Statistical analysis

For each landscape scenario, GENESYS was configured to produce a summary output in FSTAT (Goudet, 1995, 2001) format of all "living" individuals every 5 model years up until year 25 and then every 25 model years thereafter. I then used a custom script by A. Di Fiore to process these genotypes using the *hierfstat* package (Jombart, 2012) in the statistical software R version 3.0.0 (R Foundation for Statistical Computing, 2013) in order to generated measures of genetic differentiation (F_{ST}) among all pairs of social groups at each sampled model year. All pairwise comparisons between social groups separated by the same geographic distance were averaged across the different replicate simulations. I also calculate Euclidean distances among all social groups in order to conduct a simple Mantel tests to test for any correlation between geographic distance and genetic distance at each sampled model year. For the fragmented landscape, these analyses were done for social groups on the same side of the barrier and for social groups separated by the barrier. Additionally, for the alternative scenario, I used a partial Mantel Test to decompose the relative contribution of the geographic barrier versus a process of isolation by distance (IBD) to explain the genetic structure seen in these simulated social groups. In this case three different matrices were compared: (1) pairwise F_{ST} between social groups, (2) pairwise geographic distances between social groups and

(3) a pairwise binary matrix coding the position of each population pair relative to the matrix (populations on the same forest patch 0 and on different forest patch 1). Mantel and partial Mantel tests were performed using the software FSTAT (Goudet 1995) with 10,000 permutations. For simplicity, I present geographic distance for this analysis in terms of "home range separation" (HRS) distances – i.e., the minimum number of edges separating two home range centers on the initial hexagonal network of group positions. On a regular, hexagonal grid containing 36 groups, multiple pairs of groups are separated by between 1 and 7 edges, while a single pair of groups (located on set of diagonally opposed corners of the group) is separated by 8 edges. I excluded data from this lone but maximally separated pair of groups from our analyses. Furthermore, since at year 0, all simulations started with the same initial conditions, I did not calculate any Mantel test for this specific year, as there was only one replicate.

Moreover, I calculated pairwise estimates of relatedness (r) among all individuals present in the population every 5 model years up until year 25 and then every 25 model years thereafter years using the estimator of Queller and Goodnight (1989), as implemented in R code distributed by K. Csillery (2006). These were then averaged among females and among males within each social group (WSG) and between social groups (BSG) at each sampling point for each simulation and summarized across simulations. I used these summary data to examine how mean WSG and BSG relatedness values for males and females changed over time. Finally, for the fragmented landscape I compared average relatedness among males and among females, not only within and between groups from the same side of the barrier, but also between groups from opposite sides.

RESULTS

Null Scenario - IBD

Fst values for pairwise comparisons among simulated tamarin social groups increased dramatically during the first 25 years of the model, after which they remained relatively constant (Figure 3). The F_{ST} pairwise comparisons between adjacent social groups (HRS = 1) after year 25 were lower (~0.15) than the values observed for those comparisons among social groups separated by one or more intervening home ranges. Overall, F_{ST} values obtained for all comparisons were significantly greater than 0 indicating that these social groups are structured and genetically differentiated. The Mantel tests revealed a significant, positive association between geographic and genetic distance during every year of the simulation from model year 25 and on (Table 2).

Mean relatedness among males and among females within social groups (HR = 0) was significantly higher than that among males and among females between social groups separated by any distance at every sampling point across the simulations after year 0 (Welch 2-sample t-tests: all $P << 0.001$). Mean relatedness among males and among females within social groups increased rapidly during the first 25 model years, after which it increased only slightly (~0.28 – 0.3) (Figure 4). Mean relatedness among males and females between social groups separated by one home range increased slightly during the first 25 years after which it remained constant with a mean value close to 0.02. On the contrary, as distance between groups increased, between group relatedness decreased over time in every year from year 5 on (Figure 4). Overall, for both males and females, average pairwise relatedness among same-sexed individuals was strongly influenced by geographic distance (ANOVAs: $df = 7$, $P << 0.001$ for all sampled model years from year 5). Tukey post-hoc tests revealed that from model year 5 on the average relatedness of same-sexed animals within groups was significantly higher than that of

same-sexed animals in adjacent groups (HRS = 1) as well as more distant groups (HRS = 2 to 7). Likewise, at every sampling point from model year 10 on the average relatedness of same-sexed animals in adjacent groups also was positive and significantly greater than the average relatedness of same-sexed individuals separated by one or more intervening home ranges However between mean relatedness was not significantly different when compared among social groups separated by more than one home range. Finally, the mean genetic relatedness among males and among females, both within and between groups, did not differ significantly from one another in any year or at any separation distance for between group comparisons (Welch 2-sample t-tests: all NS)

Alternative Scenario - IBB

Average pairwise genetic distances between social groups analyzed for each population independently showed exactly the same relationship between F_{ST}, geographic distance, and time as I found in the contiguous landscape simulations. F_{ST} increased steadily during the first 25 years of the model, after which it stabilized. Likewise, the F_{ST} value between adjacent groups was significantly lower than that between groups separated by one or more intervening home ranges (Figure 5). Pairwise comparisons between social groups in different populations separated by a barrier, on the contrary showed a different pattern. Average F_{ST} values for pairwise comparisons among groups on opposite sides of the barrier jumped from 0 to ~0.19 during the first 25 model years and continued to diverge over the remaining years, reaching a Fst values of ~0.47 by model year 200 (Figure 6). It is important to note that irrespective of the distance between social groups on opposite sides of the barrier all comparisons among social groups were very similar (Figure 6). The distance between groups on opposite sides of the barrier had

no effect on their degree of genetic differentiation: groups separated by 7 home range edges were no more genetically distinct than groups separated by a single home range (Figure 6).

There was an observable significant positive correlation between genetic and geographic distance, as predicted by an isolation by distance model, for sets of social groups located on each side of the river (Table 3). Nonetheless, a positive non-significant correlation was observed for population 1 on year 125 of the model and for population 2 on year 175. By contrast, the correlation between genetic distance and the binary matrix (coding the position of the social group relative to the barrier) revealed that, after year 75, more than 90% of the variance in genetic distance among groups in the fragmented landscape was due to the effect of the barrier. In no year was geographic distance significantly correlated with F_{ST} once location was controlled for, except at year 25 where a positive correlation was observed (Table 4). In isolation by barrier model, it is expected to observe two different clusters of F_{ST} values corresponding to 1) social groups in the same population and 2) social groups from populations separated by a barrier. Additionally, it is expected to observe significantly higher F_{ST} values between social groups separated by the barrier than F_{ST} values between social groups in the same side of the barrier or from the same population. When genetic distance was plotted against geographic distance, it was possible to observe a perfect isolation by barrier model, as irrespective of the geographic distance, F_{ST} among social groups on opposite sides of the did not vary (Figure 7).

Average relatedness among males and among females from the same group increased rapidly within the first 25 years of the model, and continued to increase steadily in subsequent model years growing to a value of ~0.5 by the end of the simulation without reaching an asymptote. Likewise, mean relatedness between same sex individuals

in different groups located in the same side of the barrier also increased steadily over time (Figure 8). Finally, between group mean relatedness among males and among females decreased dramatically over time up to ~-0.4, with no observable effect of geographic distance (Figure 8).

DISCUSSION

The primary goal of landscape genetic studies is to infer a correlation between the processes of gene flow in a landscape and the subsequent pattern of genetic variation that arises over time (Holderegger and Wagner, 2006). However, the potential of this emerging field to inform the effects of, for example, habitat fragmentation on the movement of individuals is dependent on the accuracy of the inference relating landscapes to gene flow. This information is especially important for endangered species living in highly fragmented landscapes.

Sex specific characteristics, such as sex biased dispersal and philopatry, have been shown to influence gene flow, and thus spatio-genetic structure within and between populations (Avise, 1994; Melnick, 1987; Storz, 1999). In primates, these aspects of the social system, which are products of the differences of behavior among individuals and between the sexes, have profound consequences for the genetic structure of primate populations (Di Fiore, 2012a). However how these features of social systems influence landscape genetic inferences have until now not been well explored. Therefore, in this study, the goal was to identify how certain aspects of primate social systems are expected to influence primate population genetic structure and in turn landscape genetic inferences, using as an example tamarin primates.

The particular breeding system observed in Callithichines – characterized by high male and female reproductive skew, coupled with the short dispersal distances observed in these species – has been seen to lead to fine scale structure (Huck et al., 2007). If the above mentioned factors influence how tamarin populations are structured, it is important to note then that more variables besides the landscape, per se, should be considered in landscape genetic studies as possible additional influences on genetic differentiation. It is

important, then, to include additional causal mechanisms (i.e. mating system) as a model variables, rather than focusing just on a single type of variable (landscape features) that could potentially misinform our conclusions.

In the case of tamarins, if the mating system rather than the landscape *per se* is the major mechanism driving population structure, we would expect to see the same pattern of genetic structure arise in both the fragmented and unfragmented landscapes. Accordingly, if the mating system strongly influences the apportionment of the genetic variability in an organism, then possible effects of landscape configuration and composition on population structure could be confounded. In this simulation specifically, we would have expected to see the same pattern of isolation by distance in both simulated landscapes rather than find a stronger effect of isolation by distance model in a continuous landscape and stronger effect of isolation by barrier in a fragmented one. In other words, I predicted that the expected isolation by barrier model in the alternative scenario would have been obscured in the alternative scenario, if mating system and dispersal behavior have a greater effect on how genetic variability is apportioned in a heterogeneous landscape.

The results of the null scenario simulations are in accord to what should be expected for a primate species like tamarins characterized by a small group size, relatively high female reproductive rate, strongly skewed reproduction towards a single breeding male and female in each group, a lack of a sex-bias in dispersal, and dispersal being primarily to adjacent groups. My results showed a significant correlation between pairwise F_{ST} measures and geographic distance between social groups in the null scenario, as expected by an isolation by distance" (IBD) model (Wright, 1943). Furthermore, average relatedness within groups was much greater than between groups, and not different from that among males and among females. Within group mean

relatedness increased over time and then reached a steady state, while the between group relatedness decreased over time. These results are concordant to what would have been predicted *a priori* for a primate species following a 'stepping stone' dispersal model. As dispersal distances are short, higher F_{ST} values (and therefore greater genetic differentiation) among social groups that are farther apart should have been observed. Additionally, in a uniform, unfragmented landscape, where little habitat heterogeneity is present and individuals' movements are not restricted by barriers or inhospitable habitat types, a pattern of isolation by distance rather than a strong effect of isolation by barrier would have been expected.

For the alternative scenario, where an impassible barrier was simulated in the landscape, the same pattern of genetic variation among social groups observed in the null scenario was both predicted and observed for social groups located in the same side of the barrier. Pairwise F_{ST} values increased with geographic distance and over time, mean relatedness among males was the same as among females, and mean relatedness was greater among males and among females within groups than between groups. However, within-group average relatedness increased not only during the first 25 years of the model but continued to increase steadily through time for same-sexed individuals, and the same was true for same-sex individuals from different social groups located on the same side of the barrier. Mean relatedness between same sex individuals from different groups occupying different sides of the barrier, on the contrary, decreased over time. Furthermore, social groups located on opposite sides did not show a positive correlation between genetic and geographic distance, but on the contrary conform to an isolation by barrier model. Irrespective of the geographic distance between social groups on opposite sides of the barrier, F_{ST} values did not differ. Individuals living in a fragmented landscape composed of unsuitable habitat (such as the barrier in this case) should have movement

paths that are chosen primarily based on the permeability or suitability of the habitat, resulting in patterns of isolation by resistance or isolation by barrier (Cushman et al., 2012), as was observed in this study.

The unexpected increase of mean relatedness among males and among females within a group over time can be explained by the combination of the genetic drift populations on both sides of the barrier were experiencing and by the way in which the Queller-Goodnight (1989) relatedness estimator I used was calculated. First, with fragmentation, the genetic pools on opposite sides of the barrier are isolated from one another and evolving independently due to drift. Second, pairwise genetic relatedness among individuals between or within social groups in a population at each time step were estimated relative to background allele frequencies that were calculated for the whole set of individuals, irrespective of the side of the barrier they were from. Consequently, the relatedness estimates among individuals from the same side of the barrier in this study will inevitably be higher than those among individuals on opposite sides of the barrier. Moreover, as populations diverge over time due the barrier and experience more genetic drift, estimates of relatedness will continue to increase.

The results of this study show different patterns of genetic structure for a fragmented and for an unfragmented landscape and consequently show how genetic variation is being apportioned in tamarin primates as a consequence of the interplay between landscape features and tamarin specific mating system. The ability to predict whether or not a given landscape configuration or composition has a significant effect on genetic differentiation is relevant to conservation programs. More importantly, however, is to accurately identify the factors that are determining this genetic differentiation and thus become detectable using landscape genetic analysis. Evaluation of how well different simulation approaches perform in identifying the correct driving process

governing gene flow in complex landscapes and under what conditions is of major importance (Balkenhol et al., 2009; Cushman et al., 2012; Jaquiery et al., 2011; Segelbacher et al., 2010). The relative influence of certain aspects of social organization, particularly high reproductive skew and low dispersal abilities, on the capacity to correctly identify the correct landscape process is still not clear. Landscape genetics is a relatively new field of study and it is still unclear how mating and social system affect inferences and conclusions.

Although this study did not demonstrate a clear influence of mating strategies on landscape genetic studies conclusions, it constitutes the first attempt to understand this influence. Future studies should be expanded to compare different mating and dispersal patterns in the same landscape to evaluate the possible confounding influence of these features of social systems on landscape genetics inferences.

Appendix

Age Category	Age Classifications	Range of Ages (yrs.)	Female Fertility (# offspring)	Female Mortality	Male Mortality
1	Infant Juvenile Subadult	0.00 – 0.50 0.50 – 1.00 1.00 – 1.25	0.0	0.3000	0.3000
2	Subadult Adult	1.25 – 2.00 2.00 – 2.50	0.1	0.1500	0.1500
3	Adult	2.50 – 3.75	2.0	0.1165	0.1165
4	Adult	3.75 – 5.00	1.0	0.1400	0.1200
5	Adult	5.00 – 6.25	2.0	0.1400	0.1200
6	Adult	6.25 – 7.50	4.5	0.2000	0.1500
7	Adult	7.50 – 8.75	6.5	0.2511	0.3615
8	Adult	8.75 – 10.00	5.5	1.0000	1.0000

Table 1: Age categories used in the model and associated probabilities of female fertility and male and female mortality.

Name Parameters	*Age Classifications*
Number-pops	1 (IBD) or 2 (IBB)
Total-groups	25
Number-loci	20
Max-alleles	20
Pixels-per-step	10
Offspring-model	Female-fertility
Regulation-Model	Carrying-capacity
Mating-model	MM-dom-based
Degree-of-male-skew	1
Proportion-of-males-mating	1
Proportion-of-extragroup-paternity	0
Inbreed-w-sire- allowed	False
Proportion-of-surviving-inbreeding	0
Dispersal-model	Stepping-stone
Male-dispersal-proportion	1
Female-dispersal-proportion	1
With-dependant	False
Max-n-dispersals	10
In-migration	True
Mutation-model	Stepwise-mutation

Table 2: Parameters used to run the model. Name of parameters are shown as seen in the model.

Year	r
0	0.336
25	0.920**
50	0.875**
75	0.758**
100	0.877**
125	0.817**
150	0.942**
175	0.851**
200	0.860**

Table 3: Correlation coefficients of the Mantel test between geographic and genetic distance matrices of the null scenario (IBD). Significant values shown in bold (** $p<0.01$ and * $p<0.05$)

Year	r (Pop1)	r (Pop2)
0	---	---
25	0.873**	0.842**
50	0.866**	0.920**
75	0.819**	0.905**
100	0.869**	0.868**
125	0.621	0.842**
150	0.798**	0.780 **
175	0.832**	0.668
200	0.864**	0.882**

Table 4: Correlation coefficients of the Mantel test between geographic and genetic distance matrices for both populations present in the alternative scenario (IBB). Significant values shown in bold (** $p<0.01$ and * $p<0.05$)

Year	**IBD**	**IBB**
0	---	---
25	0.606**	0.573**
50	0.358	0.889**
75	0.2023	0.975**
100	0.187	0.979**
125	0.185	0.979**
150	0.176	0.981**
175	0.171	0.983**
200	0.184	0.981**

Table 5: Correlation coefficients of the partial Mantel test between geographic and genetic distance matrices of the null scenario (IBD). Significant values shown in bold (** $p<0.01$ and * $p<0.05$)

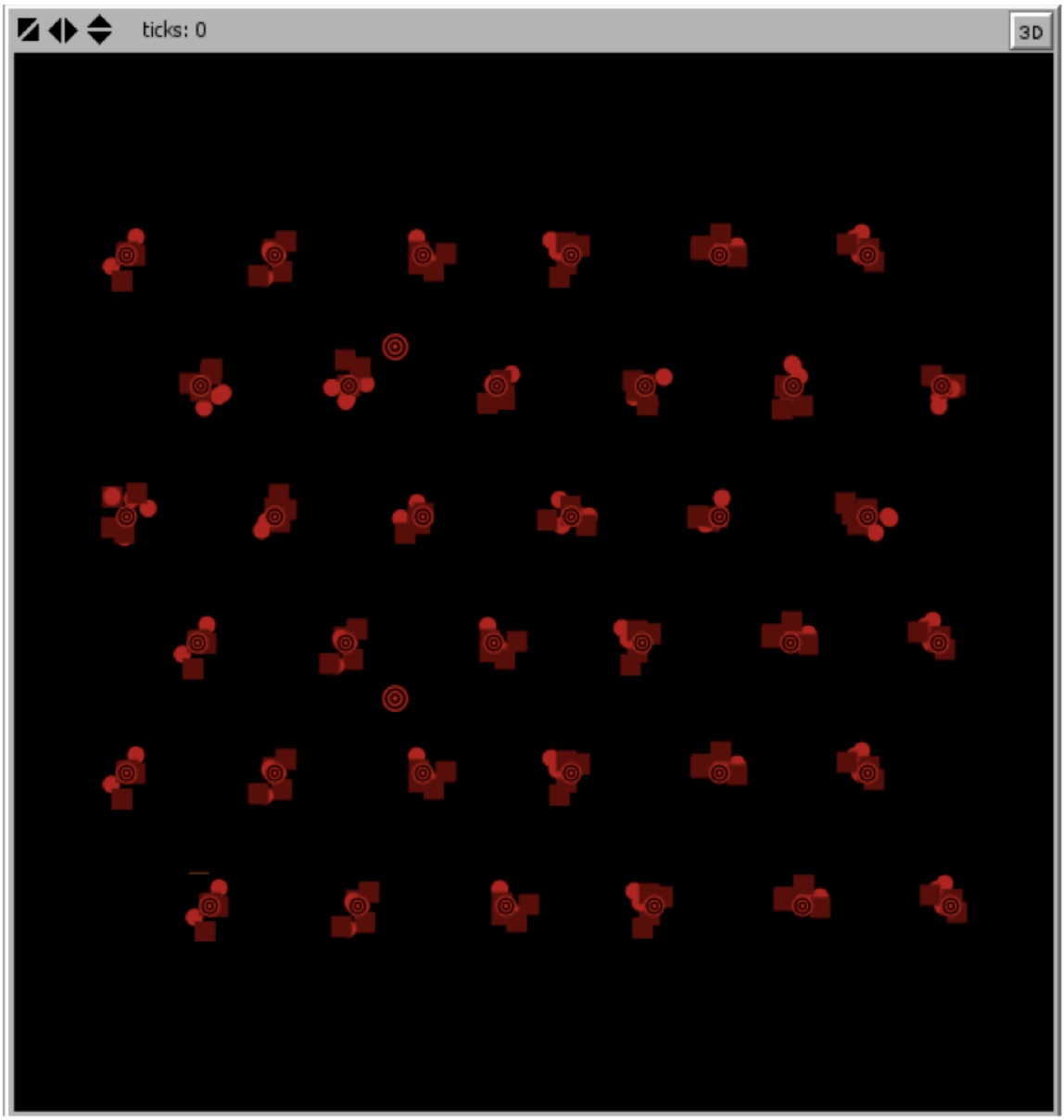

Figure 1: Simulated world of ~1600 hectares in area (or ~4000m x ~4000m) containing the home ranges (~27 ha) of 36 social groups of 'tamarins'. Each social group is depicted as an orange circle. Individuals of each social group are shown bright orange or red circles (females) and squares (males).

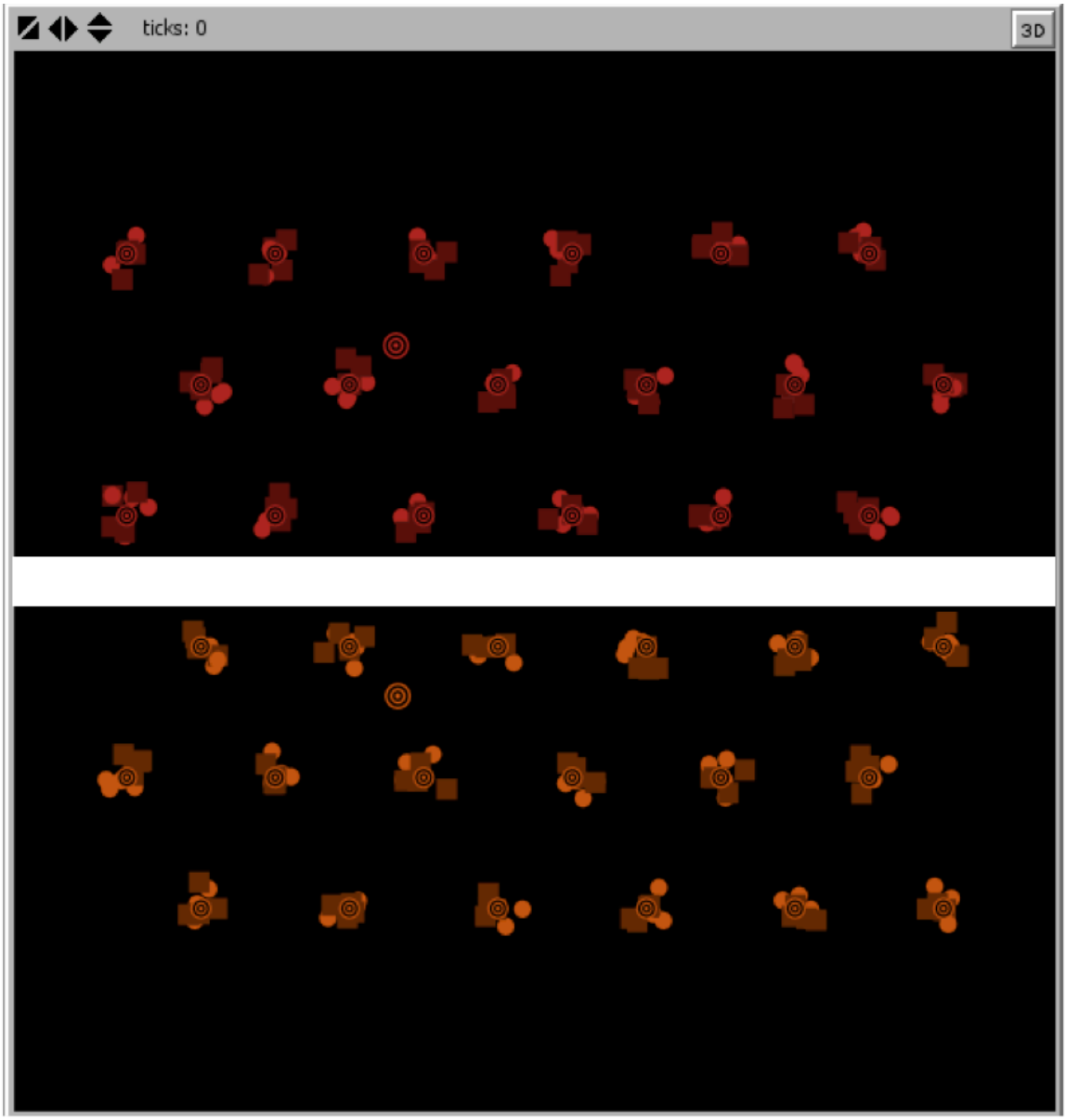

Figure 2: Simulated fragmented landscape. Each social group is depicted as an orange/black or red/black circle depending on the population they belong to. Individuals of each social group are shown bright orange or red circles (females) and squares (males). Continuous landscape is represent in black, while the impassable barrier in white.

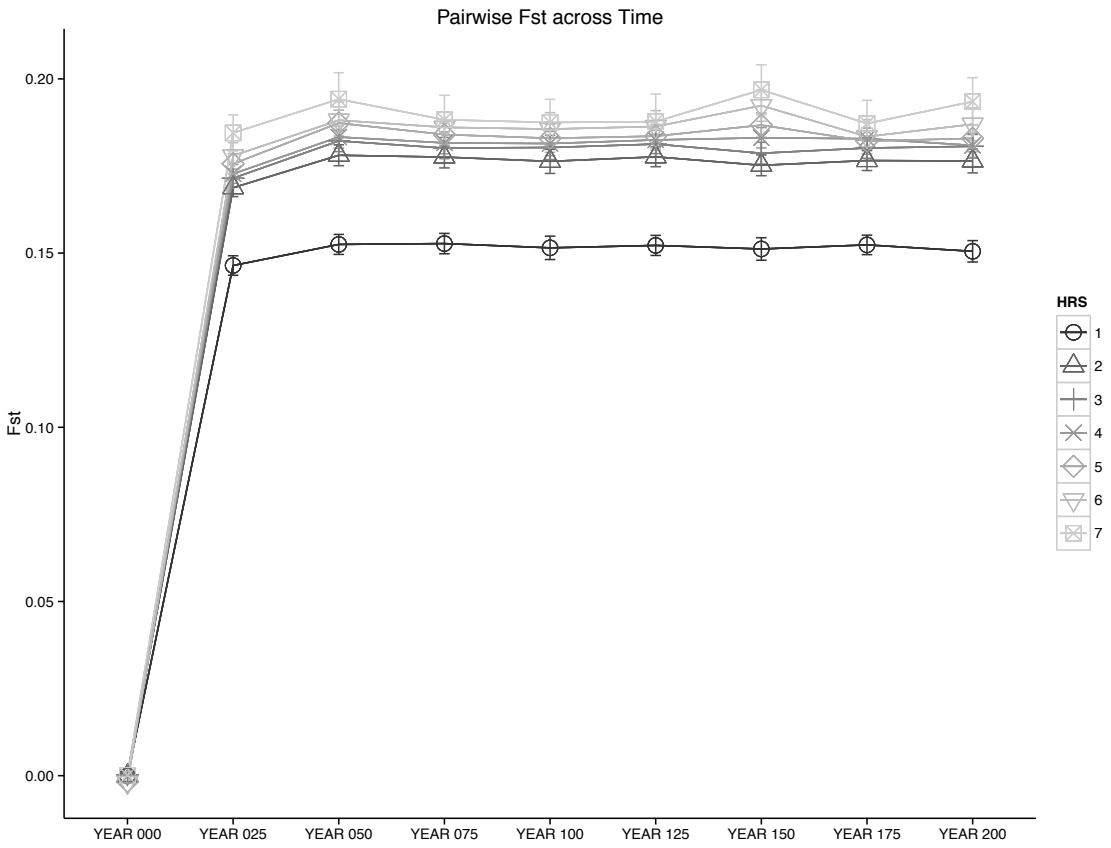

Figure 3: Average pairwise Fst values between social groups, in the null scenario, separated by different geographic distances over time. Each series represents a different geographic distance in meters among social. Error bars represent the 95% confidence interval across simulations in average F_{ST} across all pairwise comparisons for the given distance.

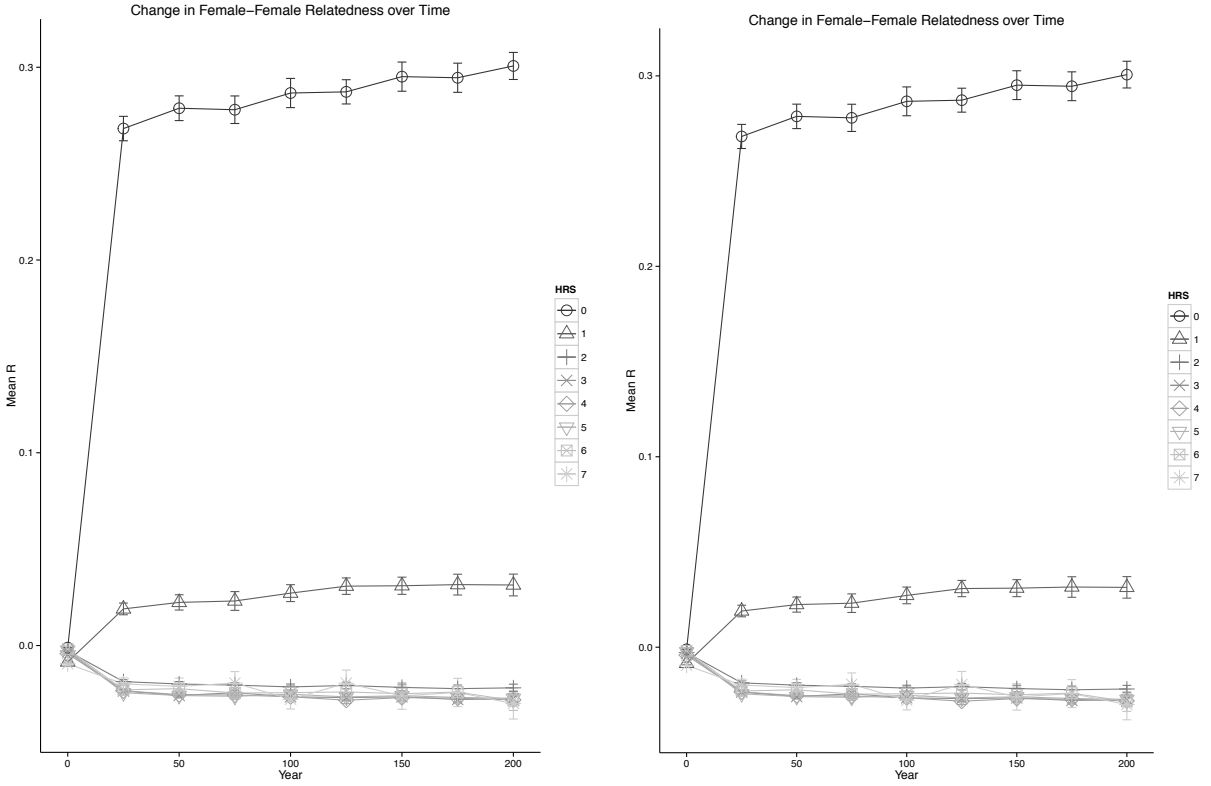

Figure 4: Change in average pairwise relatedness among males (right) and among females (left) within the same social group (HRS = 0) and between social groups separated by 1 to 7 home ranges (HRS = 1 to 7, where HRS = 1 for adjacent groups).

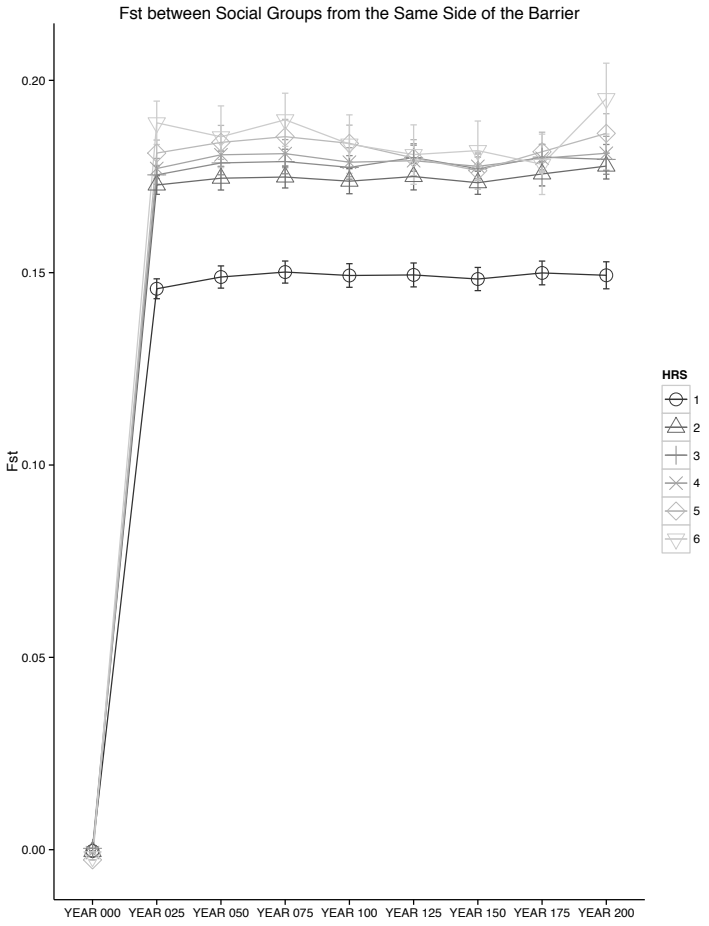

Figure 5: Pairwise Fst values over time between social groups from Population 1, in the alternative scenario, separated by different geographic distances (HR). Each series represents a different geographic distance in HR separating two different social groups. Error bars represent the 95% confidence interval across simulations in average F_{ST} across all pairwise comparisons for the given distance.

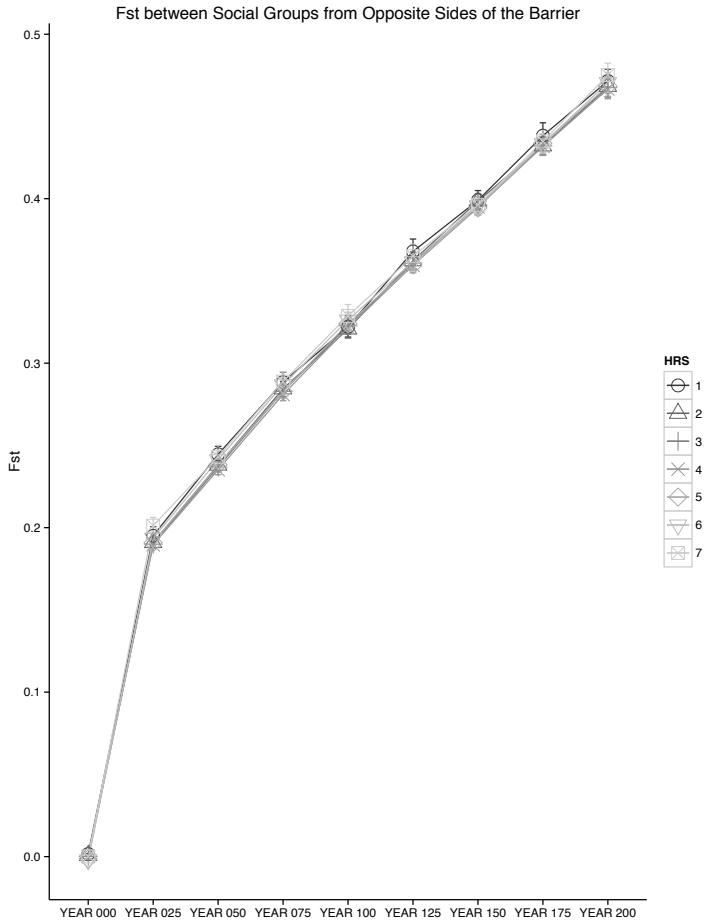

Figure 6: Pairwise Fst values over time between social groups of Population 1 and Population 2, in the alternative scenario, separated by different geographic distances. Each series represents a different geographic distance in meters separating two different social groups. Error bars represent the 95% confidence interval across simulations in average F_{ST} across all pairwise comparisons for the given distance.

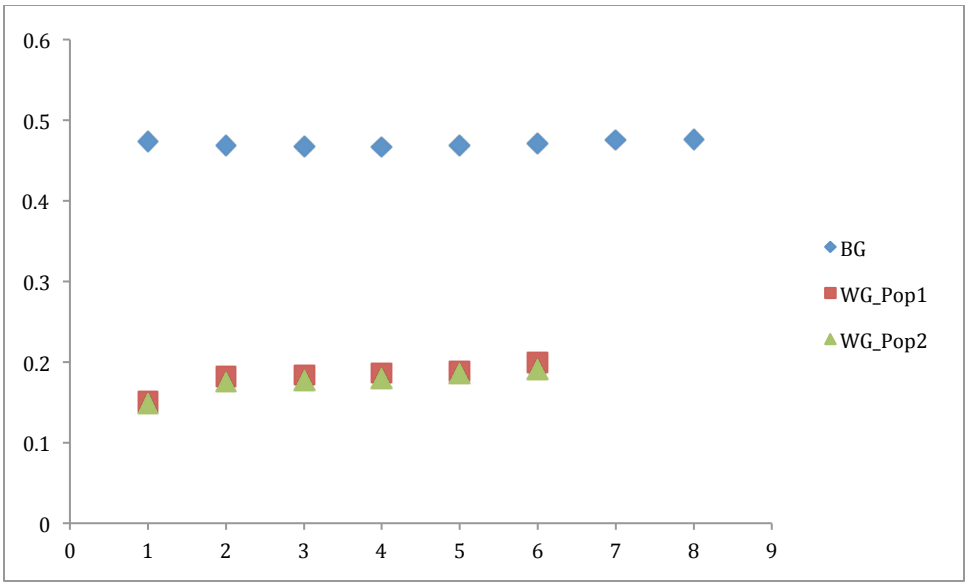

Figure 7: Correlation of pairwise Fst and geographical distances between social groups sampled in population 1 (WG_Pop1) and population 2 (WG_Pop2) and on different populations (BG). Error bars represent the 95% confidence interval across simulations in average F_{ST} across all pairwise comparisons for the given distance.

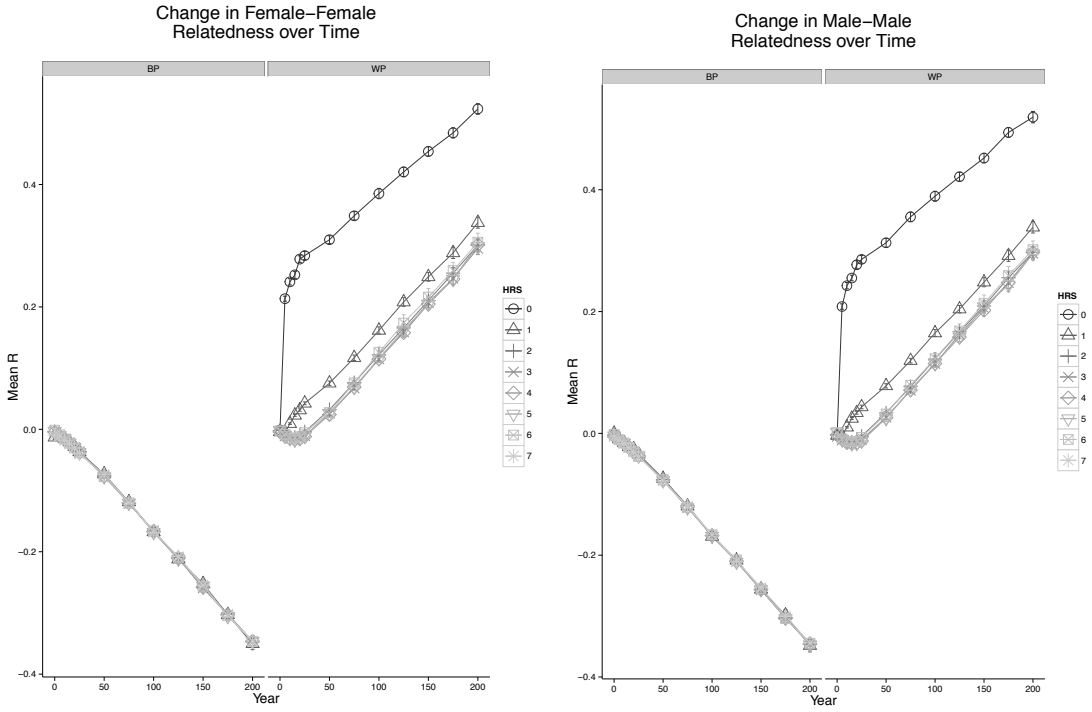

Figure 8: Change in average pairwise relatedness over time among females (A) and among males (B), both between populations (BP) and within the same population (WP) separated by a barrier in the fragmented landscape. Error bars represent the 95% confidence interval across simulations in average relatedness for the given type of pairwise comparison (sex plus distance category for each sampled year).

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